

THE SENSITIVITY OF ECHOLOCATION IN THE FRUIT BAT, ROUSETTUS

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Moehres and Kulzer (1956b) have reported that among the Megachiroptera (Old World fruit bats and flying foxes) the genus *Pteropus* orient visually while *Rousettus aegypticus* orient visually but also echolocate. Six additional megachiropteran genera, *Eidolon*, *Cynopterus*, *Ptenochirus*, *Lissonycteris*, *Eonycteris*, and *Macroglossus*, have all proved, like *Pteropus*, to orient visually and not acoustically. Observations of two additional species of *Rousettus*, *R. amplexicaudatus* and *R. seminudus* as well as *R. aegypticus*, have confirmed Moehres and Kulzer's conclusions (Novick, 1958). *Rousettus* generate clicks by movements of the tongue and emit these through the open corners of the mouth (Kulzer, 1956) rather than producing sounds laryngeally as do the Microchiroptera (Griffin, 1946, 1952; Novick, 1955; Griffin, 1958).

As far as is known at present all of the Megachiroptera except *Rousettus* are helpless in total darkness. *Rousettus* apparently make use of vision and/or echolocation depending upon the light conditions, the difficulty of their flight path, and the type of flight required (take-offs and landings, for example). The echolocation system used by *Rousettus* has almost surely evolved independently of the system employed by the Microchiroptera. Furthermore, it resembles in design the system serving much the same purpose in the cave-dwelling birds, *Steatornis* and *Collocalia*. The isolation of these three natural sonars in single genera, their simple designs, and their facultative employment (all three genera orient visually in adequate light) make it seem likely that they are recent developments compared with undoubtedly ancient microchiropteran echolocation systems. There is, therefore, considerable interest in comparing the effectiveness of the echolocation system of *Rousettus* in the detection of small objects with that achieved by the Microchiroptera, especially some carefully studied species of the families Vespertilionidae and Phyllostomatidae (Curtis, 1952; Griffin and Novick, 1955; Grinnell and Griffin, 1958).

Since the orientation clicks of *Rousettus*, *Steatornis*, and *Collocalia* are clearly audible to man, they obviously contain more energy at frequencies below 20 kc than do the orientation pulses of most of the Microchiroptera. The principal component in *Rousettus* clicks is between 12 and 18 kc, depending upon the species and the individual, but overtones and harmonics are present to a considerable degree (Novick, 1958). *Saccopteryx* and *Taphozous* (Emballonuridae) and some species of *Tadarida* (Molossidae) emit partly audible orientation cries. *Rhinopoma* also emit orientation pulses with audible components (Moehres and Kulzer, 1956a). *Rousettus*, *Steatornis*, and *Collocalia*, though, unlike all of the Microchiroptera,

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produce clicks with relatively little energy above 20 kc. Thus, it appeared that only relatively long wave-lengths would be available for echolocation and that *Rousettus* and the two cave-dwelling birds might be unable to detect obstacles as small as the wires that had been used as standardized test objects for the Microchiroptera (Hahn, 1908; Griffin and Galambos, 1941; Griffin and Novick, 1955; and Grinnell and Griffin, 1958).

A single male *Rousettus aegypticus*, captured in a dimly lighted cave at Eaux Chaudes, Katana, Kivu Province, Belgian Congo in July, 1956, was brought to Harvard University in good health in August, 1956. This bat survived for nine months on a diet of bananas and, after a short period of recuperation from its journey and its restriction to a small cage, flew skillfully in an experimental flight room 32' long, 12' wide, and 8' high. Its ability to avoid a variety of cylindrical test obstacles arranged in a row across the center of this room was tested by methods directly comparable with those previously used to measure obstacle-avoiding skill in the Microchiroptera. This *Rousettus* proved able to avoid surprisingly small wires even in total darkness. Its skill is here compared with that, measured previously, of the vespertilionid, *Myotis l. lucifugus* (Curtis, 1952).

This work was partly sponsored by the Office of Naval Research, the United States Public Health Service, and the Belgian American Education Foundation. During this time, Novick held a Post-doctoral Fellowship of the National Institute of Neurological Diseases and Blindness. We are grateful to the personnel of the *Institut pour la Recherche Scientifique en Afrique Centrale*, Lwiro, Belgian Congo for their help in capturing the experimental subject. Reproduction of this paper in whole or in part is permitted for any purpose of the United States government.

METHODS

After the bat had become accustomed to the problems of flight both in light and in total darkness in the flight room, and to the task of dodging between vertical obstacles suspended from the ceiling across the middle of the room, we tested its ability to avoid cylindrical obstacles, spaced 53 cm. apart, varying in size from cardboard tubes 5 cm. in diameter to bare metal wires 0.28 mm. in diameter. In each case these obstacles were suspended in a movable frame in a plane parallel to the end walls of the room. This plane had to be crossed by the bat in flying from its roost at one end to its roost at the other end. We forced such flights by agitating the roost which was a loosely suspended horizontal bar of wood. The bat would take off and fly the length of the room to the opposite roost or would, on occasion, make several flights back and forth before landing. In each of the tests considered below, the frame holding the obstacles was shifted horizontally in the dark just before each flight so that the absolute position of the obstacles and their location relative to the walls were unknown to the bat, though their position relative to one another was constant. Thus, the bat could not learn the location of the open spaces nor could it depend on following the walls because the space adjacent to the walls was frequently and randomly too narrow to permit passage. The room was totally dark during all these observations, but we often noticed by listening to the bat's audible clicks or to its wingbeats that it hesitated in front of the obstacles and executed dodging maneuvers to pass between them.

The *Rousettus* was thus required to fly through an obstacle plane and its accuracy of echolocation was evaluated in terms of its ability to avoid the obstacles. One must consider whether it was constantly and equally motivated to avoid collisions and whether its physical agility was sufficient for it to make the maximum use of its orientation system. The flights were scored simply as hits or misses by means of the sound of hits or in doubtful cases by inspecting the obstacles in light switched on immediately after the bat's passage. A hit always caused a clearly visible, sustained vibration of the obstacles as they were suspended from rubber bands. All hits were considered equal although some undoubtedly represented the bat's

TABLE I

Comparison of the obstacle avoidance scores of a Rousettus aegypticus with those of Myotis l. lucifugus (Curtis, 1952). The wires or other cylindrical obstacles were arranged vertically and spaced 53 cm. apart for Rousettus and 30 cm. apart for Myotis

Diameter of obstacle (mm.)		Myotis l. lucifugus		Rousettus aegypticus	
		No. trials	% misses	No. trials	% misses
Cardboard tubes	25	—	—	109	76%
Rubber tubing	19	—	—	161	78%
Rubber tubing	13	—	—	100	77%
Rubber tubing	6	—	—	50	80%
Metal rods	4.76	140	85%	—	—
Insulated metal wires	3	—	—	442	85%
Bare metal wire	1.5	—	—	200	77%
Bare metal wire	1.21	3820	82%	—	—
Bare metal wire	1.07	—	—	280	68%
Bare metal wire	0.68	480	77%	—	—
Bare metal wire	0.65	—	—	225	58%
Bare metal wire	0.46	—	—	134	45%
Bare metal wire	0.35	660	72%	—	—
Bare metal wire	0.28	—	—	50	18%
Bare metal wire	0.26	600	52%	—	—
Bare metal wire	0.12	530	38%	—	—
Bare metal wire	0.07	460	36%	—	—

inability to maneuver successfully even though it had detected the obstacle, and some represented light touches by the wingtips which may have been sufficiently painless to call for no great effort to avoid their occurrence. Unlike the Microchiroptera, this *Rousettus* rarely turned back from the obstacles. Its position and attitude in passing through the obstacle plane were recorded on about 40 flights with a camera and electronic flash. All wing positions from completely spread to considerably folded were photographed both just before and just after passage through the barrier, but we could not determine whether the bat was reducing its potential collision diameter just at the obstacle plane. Its maximum wingspread was about 75 cm., and while we cannot accurately estimate its mean wingspread this must have been at least 45 cm. or very little below the spacing between the wires.

Finally, the possibility that the bat would detect the presence of the obstacles by their fastenings to the ceiling and/or floor and learn that they were suspended ver-

tically between these two points was excluded by framing the obstacle plane with uniform fiberboard so that only the obstacles themselves and not their fastenings were exposed to acoustic or visual inspection. As a last precaution, lest the bat learn to recognize the position of the obstacles by listening to the movement of the frame between flights, the readjustment was covered with loud noise. The nature and size of the obstacles used are shown in Table I.

TABLE II

Experiments with a captive Rousettus exposed to thermal noise while flying through a row of vertical wires, 3 mm. in diameter spaced 53 cm. apart. All flights in total darkness except as noted. The noise was filtered with high pass (HP) or low pass (LP) electronic filters as noted

Date	Conditions of test	No. misses/No. trials	Per cent misses	Remarks
Apr. 23	Quiet	30/40	75%	Totally disoriented
	Noise, 25 kc HP	0/10	0	
	Quiet	17/20	85%	
	Noise, 25 kc HP with lights on	9/10	90%	Flew normally
	Noise, 15 kc LP	4/10	40%	Somewhat disoriented
	Quiet	7/10	70%	
	Noise, 15 kc LP	3/10	30%	Disoriented, but less so than at 25 kc HP
	Quiet	10/10	100%	
Apr. 26	Quiet	10/10	100%	Reluctant to fly
	Noise, 25 kc HP	0/8	0	Badly disoriented
	Quiet	6/6	100%	Very tired
Apr. 28	Quiet	8/10	80%	Badly disoriented Tired
	Noise, 15 kc LP	1/10	10%	
	Quiet	4/10	40%	
May 3	Died			
Averages of all tests	Quiet	93/116	79%	
	Noise, 25 kc HP	0/18	0	
	Noise, 25 kc HP with lights on	9/10	90%	
	Noise, 15 kc LP	8/30	27%	

RESULTS

The results are presented in tabular form. The only data excluded from consideration are those which were obtained when the bat was clearly fatigued or in poor condition near the end of a long series of trials or after many days of inactivity. The data are compared directly in Table I with similar data obtained by Curtis (1952) with *Myotis l. lucifugus*.

A short series of experiments was carried out to compare the resistance of *Rousettus* to interference with its echolocation by thermal noise but before further studies could be completed the bat died, possibly of injuries sustained in these experimental flights. The data are shown in Table II, because they indicate a mark-

edly greater vulnerability to interference by noise than occurs with the *Vespertilionidae* (Griffin, 1958). Thermal noise was generated in 20 electrostatic loudspeakers adjacent to the plane of obstacles. This noise was limited in frequency band, by electronic filters, in one of two ways. Either the filter was set at 15 kc high pass so that frequencies above 15 kc were generated at a high level while lower frequencies were attenuated progressively at 24 db per octave, or else a 25 kc low pass filter was used to transmit audio frequencies while attenuating ultrasonic components of the noise, also at 24 db per octave. Without noise, the bat avoided 3 mm. wires 79% of the time in the dark. In the light, and with the noise, in a very short series, it avoided the wires 90% of the time. But in the dark the bat was incapable of avoiding these wires at all in intense noise above 25 kc. In noise below 15 kc, it scored 27% misses. The bat's total inability to avoid large wires in noise above 25 kc and its very poor performance in noise below 15 kc suggest several hypotheses. If we assume that the poor performance was due to unfavorable signal-noise ratio at the same frequencies, then we have evidence that *Rousettus* depends upon a wide range (from less than 15 kc to more than 25 kc) of frequencies in echolocation. But alternatively the analytical ability of *Rousettus*' ears may not suffice for distinguishing a 14 kc echo from either type of noise tested, that is, we may simply have shown that the accuracy of acoustic orientation in *Rousettus* can be reduced (even totally) by noise. The results may also have been complicated by the bat's panic, discomfort, loss of motivation, or confusion in an unusual situation aside from its ability to perceive echoes in a noisy environment.

DISCUSSION

In these experiments, the wires were less widely spaced relative to the wing-spread of *Rousettus* than in Curtis' experiments with *Myotis*, but *Rousettus* almost always approached the plane of the obstacles perpendicularly while *Myotis* often approached obliquely. Our flight room was also considerably larger than the 15' \times 9' \times 6' room used by Curtis. The percentage of misses for relatively large obstacles was, nevertheless, almost exactly the same—85.0% for *Myotis* with 4.76-mm. rods and 84.5% for *Rousettus* dodging 3-mm. wires. *Rousettus* was slightly less successful at avoiding even larger obstacles (cardboard and rubber tubes) but these tests were conducted early in the bat's experience in the exacting task of flying in a dark room (with its multiplicity of echoing surfaces).

This *Rousettus* was able to detect and avoid, with a considerable degree of success, wires as small as 1.07 mm. in diameter. Only when confronted with wires of less than 1 mm. did its skill fall seriously below its own standards as well as those of *Myotis*. *Rousettus*' score decreased rather gradually. If we consider its poor performance (18% misses) against 0.28-mm. wires as due to chance, then *Rousettus* was clearly detecting 0.46-mm. wires against which it scored 45% misses. Even 18% misses against 0.28-mm. wires may have represented some degree of echolocation for, when flying in a noise field, this bat did even more poorly (100% hits) against 3-mm. wires. It seems reasonable that the ease with which a small object is echolocated depends upon its position relative to the angle of sound emission and its beaming and the angle of sound reception. Thus there is likely to be an optimal angle of approach (probably, but not necessarily, straight ahead) where the maximum echo will be received and less easily detected obstacles will be echo-

located. Obstacles which lie less optimally relative to the bat will have to have more effectively echoing surfaces to be detectable. Thus the bat might well succeed in avoiding a 0.46-mm. or 0.65-mm. wire only if it chanced to approach it favorably and so its score when working against obstacles of marginal size would be an average of chance misses, active misses, and "blind" hits. One of the limiting factors in exploring the threshold of echolocation is the danger of serious injury to the bat every time it collides with an obstacle. Such collisions may be major accidents or simply touches. Collisions with small wires tend to be more serious than those with large obstacles. *Rousettus*' performance varied considerably from trial to trial. Whenever possible we ran long series of tests and interspersed tests with 3-mm. wire between those with smaller sizes. The results were consistent with the average scores listed in Table 1.

The design of *Myotis* orientation pulses is very different from that of *Rousettus* clicks. *Myotis* pulses are produced laryngeally and emitted through the open mouth. They have a frequency modulated pattern with a gradually falling frequency starting on the average at about 80 kc and ending at about 40 kc but with beginnings ranging from at least 60 to 120 kc. Similar variety among terminal frequencies also occurs. Thus *Myotis* in single pulses and in consecutive pulses produce prominent frequencies covering about two octaves (Griffin, 1958; Novick, 1955). Furthermore, harmonics also occur in *Myotis* pulses and represent a second octave sweep within the pulses in which they occur. The importance of the harmonics as components of the outgoing pulses and the returning echoes and in the carrying of information about the environment to the bats has not been evaluated. In *Rousettus*, the pulses are produced by tongue clicks and are impure in frequency and irregular in frequency pattern. The bulk of the energy, however, appears to be in the range of about 12 to 18 kc. Additional energy is scattered from 6.5 to over 100 kc with a second maximum at about 20 to 40 kc (Moehres and Kulzer, 1956a; Kulzer, 1956; Novick, 1958).

SUMMARY

1. The ability of a single specimen of the fruit bat, *Rousettus aegypticus*, to avoid test obstacles of various sizes by echolocation in total darkness was tested. This bat avoided vertically placed 3-mm. metallic wires 85% of the time. Its success declined gradually as the wires were reduced in size but the bat displayed considerable success (68% misses) against 1.07-mm. wire and did significantly better than chance (45% misses) against wires 0.46 mm. in diameter.

2. These results have been compared with those of Curtis (1952) who studied the vespertilionid, *Myotis l. lucifugus*.

3. *Rousettus*' success at echolocation was considerably reduced when it was forced to fly in a field of intense thermal noise.

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